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Indonesian 'king of the sea' discovered

n 30 July 1998, an Indonesian population of coelacanth was discovered. It is apparently the same species as the well-known coelacanth from the Comoran archipelago in the Indian Ocean, Latimeria chalumnae Smith.

At sunrise on 30 July, Om Lameh Sonathan and his crew of ten fishermen retrieved a living coelacanth from their deep-set shark gill-net off the young volcanic island of Manado Tua, north Sulawesi, Indonesia. This is almost 10,000 km from the known population of L. chalum-

nae in the Comoros. The Indonesian specimen, which is 124 cm long and weighs 29.2 kg, was observed live by one of us (M.V.E.) for more than 3 hours before the carcass was deep-frozen and tissue samples were collected for molecular analysis.

A preliminary examination of the specimen's external morphology suggests that it is conspecific with L. chalumnae, although this must be confirmed by further investigation. The only immediately observable difference from published accounts of L. chalumnae is the colour. Previous specimens, from the western Indian Ocean, including the first one observed by Marjorie Courtenay Latimer, are usually described as 'steel blue'', although there are reports of dead coelacanths appearing brown'. The live Indonesian specimen was distinctly brown. It shares the same characteristic white mottling pattern as Indian Ocean specimens, but has numerous striking gold flecks over the entire dorsal surface of the body and fins. These are apparently a prismatic effect of light reflecting off the numerous denticles on the scales.

The fish was caught in a shark gill-net of mesh size 6 cm, approximately 150 m in length and 11 m in height, set 3.5 m off the substrate at a depth of 100-150 m for a 12-hour period overnight. The capture site was at the base of a steep volcanic slope known for its complex cave and crevice topography, and appears similar to the habitat reported for the Comoran coelacanths'

This is only the fourth coelacanth reported to be caught in a net, as the Comoran specimens were captured by fishermen hand-lining for the

The Indonesian coelacanth shortly after capture. BROWN IN COLOR]

oilfish, Ruvettus pretiosus'. Of the three previous specimens caught outside the Comoros, two were captured in trawl nets, off South Africa' and Mozambique', and a specimen from Madagascar was caught in a gill-net. Interviews with fishermen throughout north Sulawesi reveal that, although the oilfish is often caught by hand-line in this area, coelacanth (known locally

as raja laut, or 'king of the sea') are only ever caught using deep gill-nets.

The new specimen is actually the second coelacanth to be reported from north Sulawesi. On 18 September 1997, the wife of M.V.E. saw a strange-looking fish being wheeled in a cart across the fish market in Manado. The fish was immediately recognized as a coelacanth, but we only managed to take some photographs of the fish and briefly interview the fisherman before it was sold. M.V.E. has since been interviewing fishermen in villages throughout the area, as part of a US National Science Foundation international postdoctoral fellowship with the Indonesian Institute of Sciences and with the support of the National Geographic Society. These surveys have identified several fishermen from north Sulawesi who claim to have captured coelacanths. These interviews, combined with the vast distance from the Comoran archipelago, strongly support the idea that the Indonesian coelacanths are part of an established north Sulawesi population, and not simply 'strays', as has been suggested for the other specimens captured outside the Comoros'.

The discovery of an Indonesian coelacanth population has biogeographical and conservation implications. It is unlikely that living coelacanth exist only in two small, highly disjunct populations. Comparison of DNA sequences from tissues of the Indonesian and the western Indian Ocean specimens will reveal the depth of divergence between these two populations.

Further expeditions in Indonesia and to the islands in the vast stretch of Indian Ocean between the Comoros and Indonesia may discover additional populations. This would be welcome news for coelacanth conservation, as the fish is considered highly endangered, in part because of its extremely limited distribution and small population size. Nonetheless, the Indonesian government is already considering measures to prevent a repeat of the conservation problems caused by fishing and scientific collection in the Comoros".

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NATURE VOL 395 24 SEPTEMBER 1998
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A home from home for coelacanths

Peter Forey

The discovery of specimens of the coelacanth, Latimeria chalumnae, In Indonesian waters raises questions about the geographical distribution and conservation status of this remarkable fish.

In page 335 of this issue' Erdmann et al. report the existence of living Sulawesi, Indonesia, some 10,000 km east of their presumed natural home of the Comoros archipelago in the western Indian Ocean (Fig. 1). The circumstances of the initial discovery are astonishing Erdmann's wife happened to see the instantly recognizable form of a coelacanth being carted through a fish market; Erdmann and colleagues later saw and described a live Indonesian specimen.

The first living coelacanth was caught in 1938 in a shark gill-net off the mouth of the Chalumna River, South Africa, and was named Latimeria chalumnae by J. L. B. Smith. The catch raised great excitement, for two reasons. First, this was the only sur-

viving species of a lineage of fishes - the coelacanths-that originated in the Devonian, about 360 million years ago, but was thought to have become extinct in the Upper Cretaceous some 80 million years ago, the date of the youngest fossil recovered. So here was a true 'living fossil'. How had the lineage

survived for that time without leaving any trace in the fossil record?

Second, the theory of relationships prevalent in the late 1930s held that the coelacanth was a direct descendant of Devonian fish-like ancestors of the tetrapods (land-living vertebrates, including ourselves). By studying Latimeria it was expected that we might understand something about the physiology, behaviour and ecology of our own remote ancestors during the transition from life in water to life on land. From modern evolutionary analysis' it seems that the coelacanths are more distantly related to tetrapods than first thought, and that they are their modern cousins rather than their sisters (lungfishes are now taken to be the closest living relatives of tetrapods).

But Latimeria may still hold the answers to several questions. It is the only living animal to have a functional intracranial joint: that is, a complete division running through the braincase and separating the nasal organs and eye from the ear and the brain. Many Devonian fishes and primitive tetrapods had a similar intracranial joint, but the function-

Figure 1 Latimeria west and Latimeria east. The only natural home of the coelacanth was assumed to be the Comoros archipelago off Madagascar; three specimens caught elsewhere in the western Indian Ocean (capture dates shown) are assumed to be strays swept away from the Comoros by the powerful

Mozambique current. Erdmann and colleagues' announcement' of finds of coelacanths off Sulawesi, Indonesia, considerably extends the fishes' known geographical range. Given the distance between the Comoros and Sulawesi, the direction of ocean currents and the distinct geological history of the two regions, it is unlikely that the Indonesian specimens are strays.

NATURE VOL 395|24 SEPTEMBER 1998

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ing and biological significance of this structure remain obscure. Latimeria's paired fins move in a fashion that is unlike the coordination seen in most fishes but is exactly the same way as we move our arms and legs, and studies of its nervous system may help trace the beginnings of tetrapod locomotion. The ear of Latimeria is also interesting, in that there seem to be sensory areas that are precursors of structures responsible for hearing in air'.

These points of scientific interest, along with the general curiosity value of a living fossil, have caused great demand for Latimeria. Given an estimated Comoran population of just 500, and the species' low fecundity (it is a live bearer), this has been cause for concern'. The possible existence of an Indonesian population may relieve that anxiety, but equally may also mean that other fishing grounds have to be monitored.

For reasons shown in Fig. 1, it is likely that the Indonesian population is quite distinct from that in the Comoros. DNA and protein profiling should provide the unequivocal answer. If the populations are distinct, such also allow estimation of the time

work

may

that they separated. If they are not distinct, then the implication is that the species has a very broad geographical distribution (not unknown in some deep-sea fishes') and that we can expect coelacanths to occur elsewhere in the Indian Ocean, and maybe in the Pacific.

Comoran coelacanths live at about 180 metres, below the 18°C isotherm, and inhabit submarine caves formed through recent volcanic activity'. We don't know the exact ecological preference of the Indonesian coelacanths, but these too were caught around a volcanic island known to have submarine caves, and at about the same depth.

One theory for the scarcity of Latimeria is

that the species is competitively inferior and takes refuge in newly established and remote areas. Hitherto, the only known occurrence in the Comoros supported this view. But if more populations are discovered, the less likely it becomes. It could just be that Latimeria is a widespread deep-sea fish, which may explain the absence of the coelacanth lineage from the fossil record for so long because deep-sea sediments carrying remains of fossil fish are extremely rare. The Sulawesi fishermen seem to be well acquainted with the coelacanth; for instance, they have a name for it. It is amazing how the Indonesian occurrence of such a large (adults are up to 1.6 metres in length) and distinctively shaped fish should have escaped the world's attention for so long. The next step will be to estimate the size of the population. We must hope it will be large. At present Latimeria is classified under category 'K' ('insufficient known to justify conservation action'). However unfortunate many conservationists think that is, the new discovery

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underlines how little we really know about the coelacanth in particular and oceanic life in general.

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Twin planetary systems in embryo

Alan P. Boss

ize does matter, especially when it comes to radio telescopes. With a Large Array (VLA) of 27 radio telescopes yields sharper images at millimetre wavelengths than any other instrument. Rodríguez et al., reporting on page 355 of this issue', have used it to produce the most detailed millimetre-wave image to date of the L1551 IRS5 system, confirming the existence of what are probably planet-forming disks around both protostars in this binary system. Their analysis has also thrown up some surprises, and may have considerable implications for the formation of giant planets.

About 500 light years away, Lynds 1551 is an interstellar cloud of molecular gas and dust that is producing young Sun-type stars at a tremendous rate. Embedded within this active cloud is a strong source of infrared radiation, L1551 IRS5, which on its discovery was believed to be a newly formed protostar (less than a million years old) whose optical radiation is degraded to infrared wavelengths through absorption and re-

Figure Superimposed solar systems. Contours trace millimetre-wave emission from L1551 IRS5, a binary pair of forming stars. Both are surrounded by disks about as big as the orbit of Saturn, that may be forming planets. The orbits of Jupiter, Saturn, Uranus, Neptune and Pluto are shown centred on one of these stars.

emission by the intervening dust grains.

L1551 IRS5 is celebrated as the young stellar object (YSO) that yielded the first evidence for large-scale outflows of molecular gas, flowing in opposite directions from the young star[2]. These bipolar outflows are now known to be nearly ubiquitous among YSOs. But with the new observations by Rodríguez and his colleagues', L1551 IRS5 has even more reason to be celebrated.

The VLA was used in its highest-resolution configuration to map L1551 IRS5 at a wavelength of 7 mm, discerning structures as small as 7 AU (1 AU is the mean Earth-Sun distance). This resolution is about ten times better than previous millimetre-wave observations'. With such a large jump in resolution, one can expect surprises.

The new map (Fig. 1) shows conclusively that L1551 IRS5 is a binary system, with the two protostars about 45 AU apart - not a single object as was once assumed'. Furthermore, and even more importantly, there is extended emission from each of the two protostars. They both appear to be circled by protoplanetary disks about 20 AU across. As would be expected, the disks seem to be aligned with each other and in a direction
Figure 2 Exiled world? TMR-1C (lower left) might be a giant planet ejected from a system similar to L1551 IRS5.
perpendicular to the small-scale jets that are emitted by the two young stars.

The existence of these disks was suspected from previous observations. But according to the new data, their masses are surprisingly high: about 0.05 solar masses each, roughly three times higher than the previous estimate'. In contrast, disks orbiting somewhat older and more evolved YSOS- the T Tauri stars are estimated to be around 0.02 solar masses, with much of the mass thought to reside at radii greater than 10 AU (although more material could be hidden in the opaque regions close to the YSO). In any case, these observations imply that young protoplanetary disks can contain much more mass within 10 AU (the radius of Saturn's orbit) than astronomers had been willing to contemplate. As little as 0.01 solar masses might have sufficed to form the planets of our own Solar System, so the L1551 IRS5 disks have more than enough mass to form two complete planetary systems.

Some interesting physics may follow from these measurements. When a disk is massive enough and cold enough, it will be unstable to clumping caused by the self-gravity of the disk. Spiral arms and even gaseous protoplanets might then result', a rapid means of forming giant planets. With roughly 0.05 solar masses, the L1551 IRS5 disks might be able to form gaseous protoplanets in this way in their cool outer regions, although for lower-mass disks this is still less likely than the rival theory, that giant planets form by the 'bottom-up' accretion of smaller bodies.

Giant planets have been detected in orbit around four Sun-type stars that are mem-

bers of binary systems: Tau Bootis, 16 Cygni B, 55 Rhol Cancri, and Upsilon Andromedae. Clearly, the presence of a binary star companion does not inhibit the formation of giant planets, at least not for binary separations of several hundred AU or more. But with a separation of only about 45 AU, the L1551 IRS5 binary is close enough to destabilize planetary orbits of radius greater than about 10 AU. So a giant planet might form rapidly near the edge of one L1551 IRS5 disk, only to be ejected by the gravity of the other star.

That process might explain the peculiar object TMR-1C, thought by Susan Terebey and collaborators' to be a gaseous protoplanet several times as massive as Jupiter that has been ejected from the TMR-1 binary protostar system (Fig. 2). The TMR-1 and L1551 IRS5 systems are quite similar: binary protostars with separations of about 40 AU and 45 AU, respectively, both with the youthfulness of dust-shrouded YSOs. But TMR-1C could turn out to be a background star masquerading as a protoplanet. Spectroscopic observations to determine its true nature are now being made at the Keck Observatory, so we should know soon

NATURE VOL 395|24 SEPTEMBER 1998

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nature nature
COLLMANTEL HOUR
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24 September 1987

Vol. 329 No. 6137
First pictures of the coelacanth - the 'living fossil' fish swimming in its natural environment. The photographs were taken from a mini-submarine, near the islands of the Comores in the Indian Ocean, at a depth of 200 m. See page 331.
Retroviral proteases
OPINION
GEOLOGY LIBRARY
SG GUYOT HALL
PRINCETON UNIVERSITY
A good week for the world
NEWS
East-West technology US national laboratories pro-nuclear tests Launcher developments in France and India UK space lobby Now for the greenhouse Hackers' success Vatican observations Sellafield tunnel Hepavax B Post-Chernobyl limits UK clinical research Australian budget Awards time Human genome sequencing Cornell and Stanford universities' building
CORRESPONDENCE
South Africa
274-281
THIS WEEK
Millisecond pulsars
The discovery of a millisecond pulsar without a binary companion is provoking a reconsideration of theoretical models, pages 309, 310, 312 and 285.
Tree-species richness
The diversity of tree species may be limited by the local availability of energy, pages 326 and 292.
✔Sulphur emissions
Oceanic dimethylsulphide emissions could be involved in climate control through a cloud albedo feedback mechanism, page 319.
Predicted earthquake
Analysis of a successful prediction, based on observation of previous seismic quiescence, of an earthquake, on the San Andreas fault, page 323.
Guide to authors

Modelling suggests that retroviral proteases, including that of the human immunodeficiency virus, correspond to a single domain of an aspartic protease, page 292.

Receptor identity

Structural and biochemical features of the insulin-like growth factor II receptor appear identical to those of a mannose-6-phosphate receptor, page 301.

Isolated populations

Inbreeding in lions is associated with defects in gametes and changes in concentrations

See this issue, facing page 283 of circulating testosterone,

or Vol. 328 page 182.

page 328.

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Robert W Cahn
Creationism survives NASA's success
282
NEWS AND VIEWS
Prospects for fifth force fade
283
Novel model for cavity lattices
284
New millisecond pulsar in an unusual environment
David J Helfand
285
Molecular biophysics: Going round in receptor circles
Arthur Karlin
286
Mass extinctions: Confusion at the boundary
Stephen K Donovan
Coelacanth
-288

What maintains the frequencies of human genetic diseases?
Jerome I Rotter & Jared M Diamond
289
Site-specific recombination: Making Holliday junctions
David Leach
290
Nuclear structure: High spins stretch the limit
291
What makes a forest rich?
292
JD Garrett
Peter D Moore
SCIENTIFIC CORRESPONDENCE
✓ Detection of global carbon dioxide effects
SB Idso
293
Detection of sickle cell anaemia and thalassaemias
FF Chehab, M Doherty, S Cai, Y W Kan, S Cooper
& EM Rubin
293
Visna and myelin basic protein
PR Carnegie & MJ Weise
294
Enzyme identity maintained
RB Freedman
The last ribo-organism
294
295
SA Benner & A D Ellington
Amino-acid sequence similarities
SC Bell & JW Keyte
296
NEW JOURNALS REVIEW
The invisible made visible
HV Wyatt
This issue contains reviews of new journals which appeared between June 1985 and May 1986. The reviews begin on page 359 with an introduction and index on page 358
COMMENTARY
Lead and child development
357
J Michael Davies & David J Svendsgaard
297
Contents continued ■

[PAGE BREAK]

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✓ Locomotion of the coelacanth Latimeria chalumnae in its natural environment

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The coelacanth Latimeria chalumnae is the only living relic of a fossil group of crossopterygian lobe-finned fish. We describe observations of its locomotion in a natural environment using six individuals observed from the research submersible Geo in the Indian Ocean at a depth of between 117 and 198 m. Past speculation on the pattern of locomotion has included crawling with the paired fins on the rocky ocean bottom, stalking like a large piscivorous grouper, or even fast swimming in open water. Our observations show L. chalumnae to be a nocturnal piscivorous drift-hunter, moving very slowly in up- or downwelling currents, while paired fins stabilize and correct the drift motion. Paired and unpaired lobed fins are able to generate thrust. Fast starts are performed with the large caudal fin. Paired fins were not used for locomotion along the bottom. They alternate synchronously in a

pattern common in tetrapod locomotion.
L. chalumnae is found near the remote volcanic islands of the Comores in the Western Indian Ocean at a depth of -200 m. Since their discovery in 1938 no observations of free-ranging fish in their natural environment have been made, although locomotory patterns have been observed on line-fished individuals taken to the surface and released in shallow water (refs 7-9, J. L. Geraud, personal communication). These studies indicated a great flexibility of the second dorsal and anal fins which produced some forward thrust by sculling action. The paired fins did not produce swimming movements and the caudal fin did not move at all. The fish remained neutrally buoyant. Line-caught coelacanths are probably under extreme metabolic stress and might suffer decompression sickness after fast surfacing
We performed 40 dives at 30 different locations around the entire coast of Grande Comore and the north coast of Anjouan and found six fish of 120-180 cm body length off a 2-km stretch of the coastline of Grande Comore. These were observed for a. Fig. 1 Contact with the bottom a, with pectoral fins folded laterally or b, with tips of both paired fins touching the bottom. c, Drifting in an upwelling current with paired fins functioning as hydrofoils: they stabilize and correct the 'underwater flying'. total of 496 min at night only, between 21:00 and 03:30, and we have used more than 300 photographs, 90 min of 16-min cine film and 30 min of videotape recording for cinematographic analysis. The fish seemed undisturbed by the submersible or by the lights. Two of the six individuals were sitting on the bottom and four were in slow motion. During contact with the bottom, the paired fins were not used for any kind of locomotion. This was confirmed by a six-hour observation of a single individual. It frequently touched the bottom, either with the belly alone, keeping the pectoral fins laterally folded (Fig. 1a), or with the belly and the lobes of the paired fins together (Fig. 1b); no locomotion was observed.
All individuals took advantage of up- or downwellings and drifted slowly with the current. Both paired fins stabilized and corrected the 'underwater flying used in a bird wing fashion (Fig. 1c). During drifting, all individuals seemed perfectly oriented in that they avoided obstacles in their environment, apparently detecting them well in advance. Although no feeding

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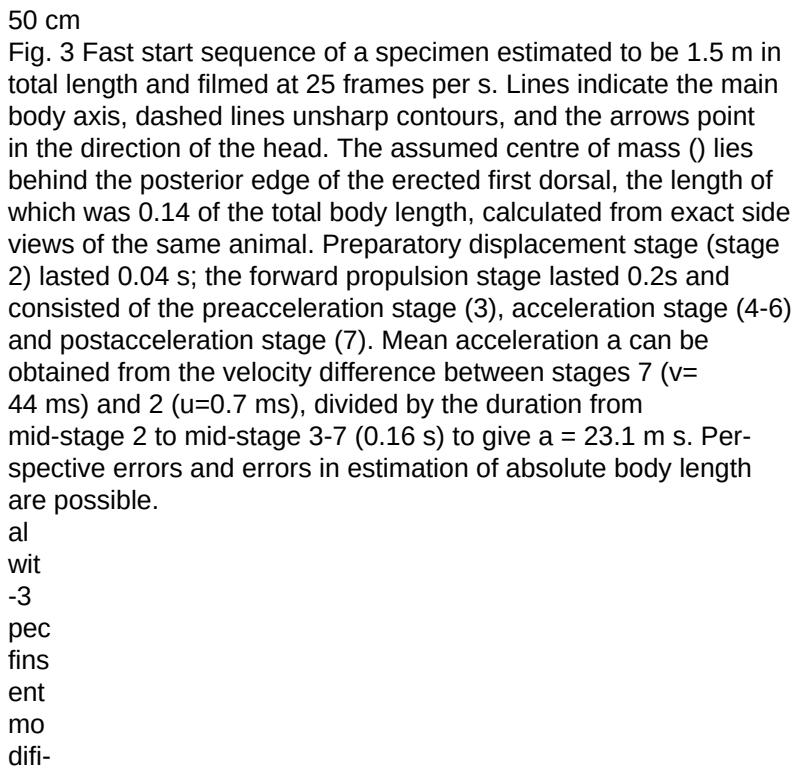

Fig. 3 Fast start sequence of a specimen estimated to be 1.5 m in total length and filmed at 25 frames per s. Lines indicate the main body axis, dashed lines unsharp contours, and the arrows point in the direction of the head. The assumed centre of mass () lies behind the posterior edge of the erected first dorsal, the length of which was 0.14 of the total body length, calculated from exact side views of the same animal. Preparatory displacement stage (stage 2) lasted 0.04 s; the forward propulsion stage lasted 0.2s and consisted of the preacceleration stage (3), acceleration stage (4-6) and postacceleration stage (7). Mean acceleration a can be obtained from the velocity difference between stages 7 (v= 44 ms) and 2 (u=0.7 ms), divided by the duration from mid-stage 2 to mid-stage 3-7 (0.16 s) to give a = 23.1 m s. Perspective errors and errors in estimation of absolute body length are possible.

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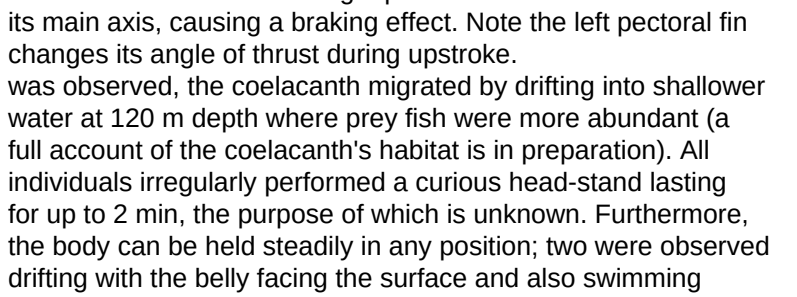
Fig. 2 Sequences of pectoral movements during a right turn. Al the beginning, the left pectoral performs a strong downward stroke while at the same time the right pectoral fin rotates 180° around its main axis, causing a braking effect. Note the left pectoral fin changes its angle of thrust during upstroke.

was observed, the coelacanth migrated by drifting into shallower water at 120 m depth where prey fish were more abundant (a full account of the coelacanth's habitat is in preparation). All individuals irregularly performed a curious head-stand lasting for up to 2 min, the purpose of which is unknown. Furthermore, the body can be held steadily in any position; two were observed drifting with the belly facing the surface and also swimming backwards. During substrate contact or during drifting, the small epicaudal lobe of the large caudal fin can be moved up to ±90° laterally to the main body axis. Although not experimentally proven, the coelacanths seemed able to detect direction and speed of the current. Their behaviour also appeared to indicate that they possess powers of electroperception, probably with the help of the rostral organ10. The drift movement was frequently interrupted by active swimming motions when the fish either changed direction or oriented itself to the bottom, using the pectoral and the unpaired lobed fins to create thrust. The pectoral fins performed a dorso-ventral up and down motion. During downstroke they are positioned obliquely against the direction of motion, but during upstroke the angle of attack is reversed. The paired fins are used as a hydrofoil. Figure 2 shows a right body turn where details of thrust-generating movements of the left pectoral are visible. Swimming

in an arc was assisted by the large expanded lobes of the caudal fin, which turned with the wave of curvature.

Four fast starts were observed: the body performed an S-shaped undulation with the caudal fin generating the main thrust (Fig. 3). Acceleration during one fast start, lasting 0.24 s. was calculated. The mean acceleration was 2.4g, which can be compared with the value for a pike of 1.1g and for a trout of 4.9g (refs 11, 12). Each pair of lobed fins, and the unpaired fins, can move at various stroke frequencies, which increase with swimming speed. During slow forward motion, paired fins had an identical stroke frequency, with unpaired fins slightly faster. During fast motion the frequencies of the pectoral and pelvic fins were again similar, but the unpaired fins were slower.

Figure 4 shows fin coordination and phase relationships during slow forward motion. The pectoral fins were synchronized

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Fig. 4
Fin coordination during slow forward motion. The movements of the fins were measured as angles, the fish being filmed from behind with all fins visible (see diagram) taking the angle between the fin tip and a vertical line through the centre of mass (see Fig. 3 symbol,). Angles: a, fin angles of right body side counting counterclockwise; B, fin angles of left body side counting clockwise; B, for unpaired median fins. Time in seconds is measured after the start of movement. The data points between 7-12s are more dense because this range was at first analysed from every third frame, but later every fifth frame was used.

Angle (degrees)
120
60

120
60
180
60
300
LETTERS TO NATURE-
right
333
pectoral
Jeff
pelvic
left
Decioral
right
pelvic
second
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180°
andi
10
12
14
15
18
20
Time (s)
with a phase difference of approximately half a cycle (180°; -3.8 s); the same relationship held for the pelvic fins. The left pectoral and right pelvic, and the right pectoral and left pelvic fins were synchronized. The synchronization was stable for the entire film sequence (more than 2 min). During fast forward movements, however, phase differences increased between different fin types, so that alternating coordination between opposite, paired fins became less precise.

Our time-limited observations confirm that all paired and unpaired lobed fins of L. chalumnae are adapted for slow swimming. They are able to produce forward thrust. Paired fins are not used for locomotion on the bottom, such as crawling or stalking. Thus the locomotory pattern of the coelacanth does not confirm early predictions. Yet the alternating coordination of the paired fins is a pattern common in tetrapods and a few bottom-living fish 13.14, including lung-fish (H. Greenwood, personal communication). The function of this neuromuscular coordination for alternating fin movements has yet to be demonstrated. Probably alternating fin movements achieve a better stabilization of the heavy, cigar-shaped body. Such coordination could indicate another preadaptation in the crossopterygian group that could have facilitated the transition to locomotion on land 15-18

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a■-Adrenoceptor subtypes linked to different mechanisms for increasing intracellular Ca2+ in smooth muscle

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Receptor-mediated increases in intracellular Ca2+ levels can be caused by release from intracellular organelles and/or influx from the extracellular fluid. Noradrenaline (NA) released from sympathetic nerves acts on a■-adrenoceptors to increase cytosolic Ca^{2+} and promote smooth muscle contraction'. In many cells activation of a■-adrenoceptors causes formation of inositol 1,4,5-trisphosphate which promotes Ca2+ release from intracellular stores. The mechanism by which receptor activation opens cell surface Ca2+ channels is not known, although in some cases it may be secondary to formation of inositol phosphates or release of stored intracellular Ca2+ (ref. 3). However a,-adrenoceptors have recently been shown to have different pharmacological properties in different tissues, and it has been proposed that different a-adrenoceptor subtypes may control mobilization of intracellular Ca2+ and gating of extracellular Ca2+ influx 7.9.10-12. We here report evidence for two subtypes of a,-adrenoceptors which cause contractile responses through different molecular mechanisms. One subtype stimulates inositol phosphate (InsP) formation and causes contractions which are independent of extracellular Ca2+, and the other does not stimulate inositol phosphate formation and causes contractions which require the influx of extra-

cellular Ca through dihydropyridine-sensitive channels. These results suggest that neurotransmitters and hormones may control Ca2+ release from intracellular stores and influx through voltage-gated membrane channels through distinct receptor subtypes.

In our previous studies", we found that the irreversible alkylating agent chlorethylclonidine' inactivated only a subpopula-

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✓Mass extinctions

NEWS AND VIEWS-

Confusion at the boundary

Stephen K. Donovan

IT IS fashionable to examine geological boundary sections in search of geochemical anomalies, such as the iridium peak of possible extraterrestrial origin that was discovered at the Cretaceous/Tertiary boundary'. Most of the boundaries that have been investigated are associated with mass-extinction events (see my recent News and Views article), but there is one horizon that has excited particular interest. This is the Precambrian/Cambrian (PE/E) boundary, at about 570 million years ago, that immediately preceded the great radiation of the first shelly faunas following the genesis of metazoan organisms in the late Precambrian. It has been suggested variously that this boundary does' or does not represent a mass extinction. There are two problems in such discussions: the actual level of the boundary has not been defined internationally; and, more seriously, a mass extinction can be recognized only if a

V FIRST OBSERVATIONS ON A LIVING COELACANTH

READERS of the paper by H. Fricke et al. on locomotion of the coelacanth Latimeria chalumnae (page 331 of this issue) may be interested in this dramatic account by J. Millot of his attempts to obtain a living coelacanth for investigation.

Throughout the night which the delighted population of Mutsamudu passed in singing and dancing to celebrate the capture the Coelacanth was watched over with admirable care. It seemed. although quite bewildered at

the sequel to its ascent to the surface. to be taking the situation very well, swimming slowly by curious rotating movements of its pectoral fins, while the second dorsal and anal, likewise very mobile, served together with the tail as a rudder.

After daybreak it became apparent that the light, and above all the sun itself. was upsetting the animal very much. so several tent canvases were put over the boat to serve as some kind of protection. But despite this precaution and the more or less constant renewal of the water, the fish began to show more and more obvious signs of distress, seeking to conceal itself in the darkest corners of the whaler.

At 14.45 hr. it was still swimming feebly; but at 15.30 hr. it had its belly in the air and only the fins and gill-covers were making agonized movements. It was then covered with a sheet and taken immediately to the hospital. There was not a scratch on it. apart from a tiny incision in the centre of the anterior part of the floor of the mouth made by the fisherman when re-covering his hook.

It measured 1.42 m. in length and weighed 41 kgm. Chemical and histological investigations could be made under the best possible conditions on perfectly fresh tissues

From Nature 175, 362. 26 February 1955.

significant faunal turnover is detected, which is difficult in strata where fossils are already so sparse. A new compilation of data by Crimes, concerning faunal activity around the PE/■ boundary, suggests that metazoan behaviour was little affected by any faunal turnover.

There are essentially two forms of fossil, body and trace fossils. As the name implies, a body fossil comprises the remains of the body of an organism, such as the shell of a mollusc or the skeleton of a dinosaur, and almost invariably comprises only the hard, skeletal parts of an organism, although soft tissues and soft-bodied organisms have been preserved in exceptional circumstances. In contrast, trace fossils represent the activities of organisms: tracks, trails, burrows, borings, fecal material are all examples, but the identities of trace-producing organisms are usually impossible to ascertain. Many traces were formed by soft-bodied organ-

isms that are not otherwise preserved. Additionally, one organism may produce different traces, and a single trace morphology may be common to several forming organisms. Many marine traces, however, have a form influenced by the environment, so although the fauna has changed drastically since the PE/€, many trace fossils are essentially unaltered.

Geochemical evidence suggests that various significant events related to organic productivity occurred close to the P■/€ boundary. But different rock sequences give different patterns of geochemical fluctuation. Tucker' found a "C carbon-isotope peak just below the level of the first trilobites in Morocco. This peak could indicate an increase in organic productivity corresponding to the early Cambrian radiation of metazoans. associated with increased plankton diversity, which could approximately correspond to the Tommotian/Atdabanian boundary (see figure).

Magaritz et al., however, found a "C peak immediately below the Vendian/Tommotian (= PE/E?) boundary in Siberia, followed by a sharp decrease at the boundary and a second, smaller peak early in the Tommotian. The decline between peaks could indicate a decrease in organic productivity, if not an actual extinction event. Hsu et al.' suggested that an iridium anomaly associated with a sharp decrease in 'C found in the Tommotian or Atdabanian of China could be related to a bolide impact and mass extinction.

Others have pointed out that the iridium peak occurs during a period in

PERIOD
AGE
Aldabanlan
Cambrian
Vendian
Tommolian

Stratigraphic units around the Precambrian/Cambrian (PE/E) boundary, marked by the arrow. Some authorities would place it in the Tommotian. The age of the boundary is between 590 and 550 million years.

which the organisms that produced small shelly fossils were radiating, before the appearance of the trilobites. By this time, the late Precambrian soft-bodied fauna had gone into decline". The new work of Crimes shows that other soft-bodied organisms left a good fossil record across the P€/■boundary in the form of plentiful trace fossils at several localities. Some groups of trace fossils are limited to the late Precambrian but many originated in the late Vendian and in the Tommotian, and continued through most or all of the Phanerozoic. The general pattern is undoubtedly one of increasingly diverse metazoan behaviour (presumably indicating a related radiation of the metazoans) from the late Precambrian and into the early Cambrian, before the appearance of the trilobites. Indeed, the first trilobite trace fossils pre-date the earliest trilobite body fossils, suggesting that soft-bodied trilobites arose very early in the Cambrian or even in the late Precambrian.

Thus, the earliest trace fossils, which record the diversification of the primitive metazoans as a function of their increasingly varied behaviour, show a similar pattern of increase across the P■/€ boundary to the small shelly fossils. Whatever we read into the geochemical anomalies, our interpretation of mass extinction must depend upon changes seen in the fossil record. Both body and trace fossils, as well as carbon isotopes. show a pattern of distribution across the PE/■ boundary that suggests the early metazoan radiation was not punctuated by the hiccup of an extinction event.

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